

# Fish and amphibians as bat predators

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#### ABSTRACT

Although bats (Chiroptera) belong to the most diverse mammalian orders, study of diversity of their natural predators has been seriously neglected for a long time. While some recent reviews contain comprehensive overviews of our recent knowledge on these phenomena for some animal groups, such work is still lacking for anamniotes - fishes and amphibians. Here, I am summarising bat predation incidences by anamniotes that were published in scientific journals and public web domains. I found out that at least 14 species of fishes and 14 species of frogs were observed as feeding on bats. Moreover, 7 and 16 species of bats were recorded as victims of hunting activity of fishes and frogs, respectively. Majority of localised incidences came from the New World; frog (between latitude 49°N to 28°S) attacks were distributed mainly in tropical or subtropical areas < 30° from equator (70% of all records), fish (44°N to 20°S) incidences reach same proportion in colder areas (> 30° from equator) and warmer areas. In some cases, these predators can regularly feed on bats, especially when hunting near roosting places of bats; however, with respect to number of recorded cases (21 for fishes and 37 for amphibians), bat predation by anamniotes seems to be very rare and opportunistic with only very limited influence on bat populations or their behaviour.

#### **KEYWORDS**

Amphibians – bats – diet – fishes – frogs – predation © 2015 Peter Mikula This is an open access article distributed under the Creative Commons Attribution-NonCommercial-NoDerivs license

## **INTRODUCTION**

Bats (Chiroptera) are among most taxonomically and ecologically diverse mammalian groups comprising more than 1200 recent species (Kunz & Fenton 2003; Gunnell & Simmons 2012). Although, they are the second largest mammalian order, several aspects of their life still remain only poorly understood. This particularly holds for predator–prey interactions; we had only limited knowledge on the spectrum of their natural predators over a long time (Allen 1940; Lima & Dill 1990). Nowadays, the knowledge on natural predators of bats is increasing due to several comprehensive reviews. However, these reviews include only few animal groups such as spiders (Nyffeler & Knörnschild 2013), some owls (e.g. Speakman 1991; Sparks, Roberts & Jones 2000; Roulin & Christe 2013) and diurnal birds (Mikula et al. forthcoming).

Traditionally, some life-history traits (e.g. long lifespan and small litter size) and agile flight of bats indicate successful predator avoidance by bats (Kunz & Fenton 2003). In

fact, however, it appears that bats have a variety of natural enemies (Sparks et al. 2000; Nyffeler & Knörnschild 2013; Mikula et al. forthcoming). Probably the most important bat predators are birds and especially owls, which are preying upon bats during their coincidental activity time (Speakman 1991; Lesiński et al. 2009; Roulin & Christe 2013). On the other hand, diurnal birds can represent substantial danger for daytime flying bats (Mikula et al. forthcoming), snakes and arthropods seem to be successful bat predator in the vicinity of their roosting aggregations (e.g. caves) (Molinari et al. 2005; Esbérard & Vrcibradic 2007; Nyffeler & Knörnschild 2013). Mammalian predators are, moreover, able to detect bat-roosting places based on odour clues (Threlfall et al. 2013). On patterns of bat predation by fishes and amphibians, we, however, have only limited information.

Representatives of anamniotes, fishes and amphibians, belong to the most diverse groups of vertebrates representing with approximately 33,000 and 7500 recent forms, respectively, substantial part of vertebrate species diversity (Nelson 2006; AmphibiaWeb 2015a; FishBase 2015). Although, there are most probably no specialised fish or amphibian bat predators, diversity of their feeding strategies and wide geographical distribution indicates that bats can at least occasionally fall prey to them. Specially, if we consider the fact that numerous larger fishes and amphibians are known to supplement their diet by preying on terrestrial vertebrates such as lizards, birds and mammals (Gregg 1945; Lowe et al. 1996; Merritt 2014; O'Brien et al. 2014; Schalk et al. 2014). Moreover, some fishes are even able to catch flying vertebrates such as birds on wing when skimming over the water surface (O'Brien et al. 2014) and can thus represent risk for therein foraging or drinking bats. Predation on bats by anamniotes is, however, infrequently described in literature. According to my best knowledge, most comprehensive review on chiropterophagy by anamniotes was published by Sparks, Roberts & Jones (2000) that included only five and two species of North American fishes and frogs, respectively. It thus seems that bat predation events by anamniotes are rare. However, no review on global scale is available. The aim of this study is thus to comprehensively review and synthesise published information on bat predation by fishes and amphibians.

## 1. METHODS

To obtain relevant information on bat predation by fishes and amphibians, I started with an extensive study of bibliographic sources. Primarily, I included cases where predators (fishes or amphibians) were observed as consuming (or at least trying to consume) prey (bats) that was alive when the predator first attacked it (Begon et al. 2005). However, it cannot be ruled out with certainty that some records represent consumption of already dead bats (necrophagy) due to the fact that in many cases, fishes and amphibians were observed as already consuming bats with no information on manner how they got to their bat prey.

The internet-based search utilised mainly the Thomson-Reuters (Web of Science, Zoological Record) and Scopus databases, Google Scholar and Google Books. When a suitable paper was selected, its references (backward search) and citation records (forward search) were used to search for other relevant articles. Additionally, I included internet search mainly for images and videos carried by Google, Google images, Flickr and YouTube to obtain maximum information on such events. Search was hold not only in English, I also included some European (German, French, Spanish, Portuguese and Russian) and Asian languages (Chinese and Japanese) as languages used in scientifically well active countries or frequently covering large areas in species-rich regions of Central and South America, Africa and Asia. In general, my searching phrase contained Latin (e.g. Hucho or Rhinella) or national genus / family / order names (e.g. catfish and toad in English) of fishes and amphibians and one of the following word combinations 'bat' or 'bats' in each of the aforementioned languages. I was particularly careful when searching among fish and amphibian groups where, due to dietary demands and morphological and behavioural adaptations, there was increased probability of being bat predator. My search was, however, restricted by my knowledge of particular languages; this holds mainly for Asian languages. Whenever I found secondary report on this topic, I tried to get as near as possible to the primary source. If I was able to find the original source of report, secondary reports were not included in the review, which otherwise were treated similarly to the primary records. When it was very probable that multiple sources were describing the same predation event, I grouped them under a single case with several references. Moreover, to obtain data for natural predation as relevant as possible, I excluded cases where anamniotes, kept as pets, were fed by bats in captivity by their owners.

# 2. RESULTS

### 2.1. Fishes

Altogether, fish predation on bats was recorded in 21 cases. Bats were found as a prey of 13 identified Osteichtyes fish species from six families of Teleostei clade (Centrarchidae 2 spp., Ictaluridae 1 sp., Lutjanidae 1 sp., Osteoglossidae 3 spp., Salmonidae 5 spp., Serrasalmidae 1 sp.); in four cases, fishes were identified at least to order level; in one case, it was taxonomically unidentified (Table 1, Fig. 1). Most bat predation attempts were recorded for Salmonidae (39% of all taxonomically identified cases) and Centrarchidae (28%), followed by Osteoglossidae (17%), Ictaluridae, Lutjanidae and Serrasalmidae (5.5% in each case). Only one evidence for bat predation by Chondrichthyes fish included *Galeocerdo cuvier* (Carcharhinidae) (Table 1).

The vast majority of recorded bat-eating fishes live in limnetic ecosystems, only G. cuvier is mostly marine and other species, Lutjanus griseus (Lutjanidae), often penetrates from marine environment to brackish and fresh waters. Except for five records from Eurasia (24% of all records) and one from Australia (5%), all other records came from the New World (71%). All localised incidences occurred between the latitude 44°N to 20°S with approximately same proportion of incidences in colder areas (> 30° from equator) and tropical and subtropical areas. However, bat predation records for Hucho taimen and Brachymystax lenok, living in central and northern Asia, indicate that some records could come even from higher latitudes (Denisova 2004; Hogan & Jensen 2013; Froese & Pauly 2015). Northernmost record with given at least approximate position is reported by Kaimov & Gairabekov (2009) and included unidentified bat as a prey of Salmo trutta (Salmonidae) from Chechen Republic (43°18'N, 45°48'W), Russia. In Nearctic region, northernmost observation of fish predation on bats came from Ruby Mountains region (40°40'N, 115°31'W), Nevada, USA, where Oncorhynchus mykiss (Salmonidae) was preying upon dead or injured Myotis lucifugus (Vespertilionidae) (Borell & Ellis 1934). Most southward records from southern hemisphere were re-

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Table 1. Reported cases of fish predation on bats based on literature and unpublished records. Question mark [?] represents cases where locality was uncertain.

Fishes		Bats		Country	Source
Species	Family	Species	Family		
Chondroichtyes					
Galeocerdo cuvier	Carcharhinidae	Pteropus sp.	Pteropodidae	Australia	Simpfendorfer (1992)
Osteichthyes					
Lepomis cyanellus	Centrarchidae	Tadarida brasiliensis	Molossidae	USA	Jones & Hettler (1959)
Micropterus salmoides	Centrarchidae	Myotis grisescens	Vespertilionidae	USA	Dean (2008)
M. salmoides	Centrarchidae	Pipistrellus hesperus	Vespertilionidae	USA	Hermann (1950)
M. salmoides	Centrarchidae	Unidentified	Unidentified	No data	InTheory (2014)
Ictalurus furcatus	Ictaluridae	Unidentified	Phyllostomidae	Belize	National Geographic (2013)
Lutjanus griseus	Lutjanidae	Erophylla sezekorni	Phyllostomidae	Bahamas	Yager & Williams (1988)
Osteoglossum bicirrhosum	Osteoglossidae	Unidentified	Unidentified	Guyana	Lowe-McConnell (1964)
Osteoglossum ferreirai	Osteoglossidae	Unidentified	Unidentified	No data	Rechi (2014)
Scleropages formosus	Osteoglossidae	Unidentified	Unidentified	No data	Ford (2013)
Brachymystax lenok	Salmonidae	Unidentified	Unidentified	Russia?	Denisova (2004)
Hucho taimen	Salmonidae	Unidentified	Unidentified	No data	Hogan & Jensen (2013)
Oncorhynchus mykiss	Salmonidae	Myotis lucifugus	Vespertilionidae	USA	Borell & Ellis (1934)
Hucho sp.	Salmonidae	Unidentified	Unidentified	Russia?	Denisova (2004)
Salmo gairdneri	Salmonidae	Unidentified	Unidentified	USA	Ingles (1947)
Salmo trutta	Salmonidae	Unidentified	Unidentified	Russia	Kaimov & Gairabekov (2009
Pygocentrus nattereri	Serrasalmidae	Unidentified	Unidentified	Brazil	Ferreira et al. (2014)
Bass	Centrarchidae	M. lucifugus	Vespertilionidae	USA	Barbour & Davis (1974); Merritt (2014)
Large trouts	Salmonidae	Unidentified	Unidentified	USA?	Murphy & Nichols (1913)
Catfish	Unidentified	Unidentified	Unidentified	No data	Smokeyrobot (2014)
Large fish	Unidentified	Noctilio leporinus	Noctilionidae	Costa Rica	Börk (2006)

corded in Rio Negro Farm (19°35'S, 56°15'W), Pantanal, Brazil, where several unidentified bat individuals were found in the stomach of *Pygocentrus nattereri* (Serrasalmidae) (Ferreira et al. 2014). In the Old World, two *Pteropus* sp. (Pteropodidae) individuals were found in the stomach of shark *G. cuvier* living near Townsville (19°15'S, 146°50'E), Queensland, Australia (Simpfendorfer 1992).

Six species of bats from four families (Noctilionidae 1 sp., Molossidae 1 sp., Phyllostomidae 1 sp., Vespertilionidae 3 spp.) were identified as prey of Osteichtyes fish predation (Table 1). In 60% of the reported cases, the captured bats remained completely unidentified. Majority of identified bats belonged to family Vespertilionidae (50%), Phyllostomidae (25%), followed by Molossidae and Noctilionidae (both 12.5%).

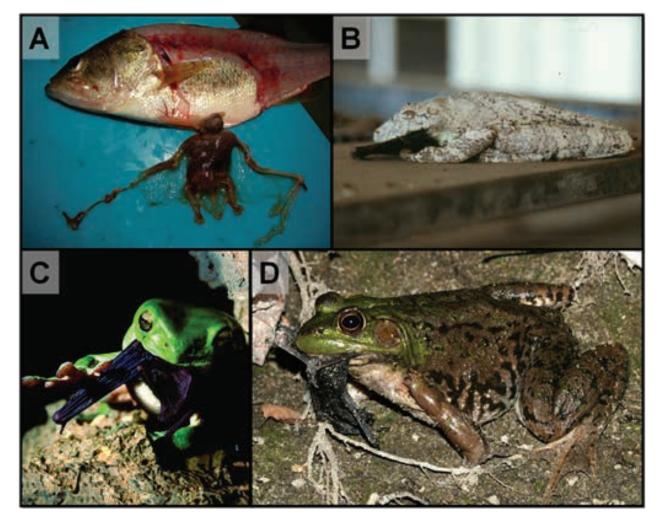


Figure 1. Examples of bat captures by fishes and amphibians. A - Stomach content of Micropterus salmoides included one partially digested individual of Myotis grisenscens, which was caught in Lick Creek conservation area, USA (Photo credit: Colby Wrasse; Dean 2008). B - Partial ingestion of unidentified bat by Hyla boans in Parque Nacional Cinaruco-Capanaparo, Venezuela (Photo credit: Albrey Arrington & Jennifer Arrington; Arrington & Arrington 2000). C - Litoria caerulea feeding on Miniopterus australis in a cave in Mt. Etna, Queensland, Australia (Photo credit: Bruce Means; Means 2003). D - Rana catesbeiana consuming one unidentified bat in the bank of the Nashua River in Lancaster (Massachusetts), USA (Photo credit: Tom Murray; Murray 2004). Reproduced with permission from all authors of original photographs.

In addition, at least one *Pteropus* species (Pteropodidae) was found as prey of Chondroichtyes fish. Altogether, identified bats made only 0.6 and 26% of global diversity of bat species and families, respectively.

## 2.2. Amphibians

Altogether, 37 cases of bat predation by amphibians were recorded. I found that at least 14 species of frogs (Anura) from five families were recognised as bat consumers (Bufonidae 3 spp., Conrauidae 1 sp., Hylidae 2 spp., Leptodactylidae 4 spp., Ranidae 4 spp.) (Table 2, Fig. 1). Highest prevalence of bat hunting records was in family Ranidae (27% of all records), followed by Leptodactylidae, Bufonidae (both 24%), Hylidae (22%) and Conrauidae (3%). I was not able to find any literature records of bat predation in Caudata and Apoda clade.

Most reports were localised in Neotropical (43% of all cases), Australian (24%) and Nearctic (22%) regions. Such

records were very rare in Europe (8%) and Africa (3%) and completely absent in Asia. Incidences were found between latitude 49°N and 28°S with ~70% of cases within warmer areas (< 30° from equator). The northernmost observation of bat predation by amphibians was published by Országhová, Mikulíček & Pachinger (2003) who reported an observation of Rana esculenta (Ranidae) feeding on Myotis mystacinus (Vespertilionidae) in Šajdíkove Humence (48°39'N, 17°16'E), Slovakia. In North America, such observation was recorded in Botany Glen (40°33'N, 85°40'W), Indiana, USA, where Eptesicus fuscus (Vespertilionidae) was observed protruding from the mouth of Rana catesbeiana (Ranidae). In Neotropics, the southernmost observation came from Curitibanos (27°17'S, 50°37'W), Brazil where one individual from Rhinella marina complex (Bufonidae) was filmed on video as eating unidentified bat (Petris 2011). From the Old World, the southernmost record came from the vicinity of Mt. Etna (23°10'S, 150°29'E),

Table 2. Reported cases of amphibian predation on bats based on literature and unpublished records. Question mark [?] represents cases where species identification was uncertain.

Frogs		Bats		Country	Source
Species	Family	Species	Family		
Bufo viridis	Bufonidae	Pipistrellus pipistrellus	Vespertilionidae	Russia	Denisova (2004)
Rhinella jimi	Bufonidae	Molossus molossus	Molossidae	Brazil	da Silva, dos Santos & de Amorim (2010)
R. jimi	Bufonidae	Pteronotus personatus	Mormoopidae	Brazil	Gouveia et al. (2009)
Rhinella marina	Bufonidae	M. molossus	Molossidae	Venezuela	Gonzalez-Fernandez (2013)
R. marina	Bufonidae	M. molossus?	Molossidae	Peru	Torres (2013)
R. marina	Bufonidae	Unidentified	Unidentified	Australia	Bierly (1998)
R. marina	Bufonidae	Unidentified	Unidentified	Australia	Richards & Hall (2012)
R. marina group (icterica?)	Bufonidae	Unidentified	Molossidae	Brazil	Srpimentelbio (2015)
R. marina group (icterica?)	Bufonidae	Unidentified	Unidentified	Brazil	Petris (2011)
Conraua goliath	Conrauidae	Unidentified	Unidentified	No data	San Diego Zoo (2015)
Hyla boans	Hylidae	Unidentified	Unidentified	Venezuela	Arrington & Arrington (2000
Litoria caerulea	Hylidae	Miniopterus australis	Vespertilionidae	Australia	Means (2000, 2003, 2008)
L. caerulea	Hylidae	M. australis	Vespertilionidae	Australia	Cray (2007)
L. caerulea	Hylidae	M. australis	Vespertilionidae	Australia	Parer & Parer-Cook (n.d. b
L. caerulea	Hylidae	Microbat	Unidentified	Australia	Macdonald (2010)
L. caerulea	Hylidae	Unidentified	Unidentified	Australia	Richards & Hall (2012)
L. caerulea	Hylidae	Unidentified	Unidentified	Australia	Davis (n.d.)
L. caerulea	Hylidae	Unidentified	Unidentified	Australia	Parer & Parer-Cook (n.d. a)
Leptodactylus fallax	Leptodactylidae	Unidentified	Unidentified	Dominica	Schwartz & Henderson (199
Leptodactylus labyrinthicus	Leptodactylidae	Anoura caudifer	Phyllostomidae	Brazil	Esbérard et al. (2006)
Leptodactylus pentadactylus	Leptodactylidae	Carollia perspicillata	Phyllostomidae	Brazil	Castro et al. (2011)
Leptodactylus vastus	Leptodactylidae	P. personatus	Mormoopidae	Brazil	Gouveia et al. (2009)
L. vastus	Leptodactylidae	Natalus stramineus	Natalidae	Brazil	Gouveia et al. (2009)
L. vastus	Leptodactylidae	Glossophaga soricina	Phyllostomidae	Brazil	Filho, Feijó & Rocha (2014)
L. vastus	Leptodactylidae	Lonchophylla mordax	Phyllostomidae	Brazil	Filho, Feijó & Rocha (2014)
L. vastus	Leptodactylidae	Tonatia bidens	Phyllostomidae	Brazil	Filho, Feijó & Rocha (2014
L. vastus	Leptodactylidae	Myotis nigricans	Vespertilionidae	Brazil	Filho, Feijó & Rocha (2014
Rana blairi	Ranidae	Pipistrellus subflavus	Vespertilionidae	USA	Creel (1963)

Rana catesbeiana	Ranidae	Eptesicus fuscus	Vespertilionidae	USA	Kirkpatrick (1982)
R. catesbeiana	Ranidae	Lasiurus borealis	Vespertilionidae	USA	Jones (1961)
R. catesbeiana	Ranidae	L. borealis	Vespertilionidae	USA	Korschgen & Baskett (1963)
R. catesbeiana	Ranidae	Myotis austroriparius	Vespertilionidae	USA	Lee (1969)
R. catesbeiana	Ranidae	Unidentified	Unidentified	USA	Murray (2004)
R. catesbeiana	Ranidae	Unidentified	Unidentified	USA	Schwalbe (2015)
Rana esculenta	Ranidae	Myotis mystacinus	Vespertilionidae	Slovakia	Országhová, Mikulíček & Pachinger (2003)
Rana pipiens	Ranidae	<i>Myotis</i> sp.	Vespertilionidae	USA	Kinsey (1961)
Rana sp.	Ranidae	Unidentified	Vespertilionidae	France	Leblanc (2005)

continued Table 2. Reported cases of amphibian predation on bats based on literature and unpublished records. Question mark [?] represents cases where species identification was uncertain.

Australia where individuals of *Litoria caerulea* (Hylidae) were photographed as eating *Miniopterus australis* (Vespertilionidae) (Means 2000, 2003; Cray 2007).

I was able to find information on 16 bat species from five families (Molossidae 1 sp., Mormoopidae 1 sp., Natalidae 1 sp., Phyllostomidae 5 spp., Vespertilionidae 8 spp.) that were identified as prey of frogs. More than 32% of all records included bats unidentified at least on family level. The majority of identifiable bats were members of family Vespertilionidae (52%), Phyllostomidae (20%) and Molossidae (16%) whereas only small number of records existed for Mormoopidae (8%) and Natalidae (4%). Identified bat taxa represent 1.3 and 26% of global diversity of bat species and families, respectively.

## 3. DISCUSSION

I found that the occurrence of bats in the diet of fishes and amphibians was very low, especially when compared to main bat predators such as owls, small carnivores and other bats, snakes and diurnal birds (Schätti 1984; Speakman 1991; Esbérard & Vrcibradic 2007; Sparks et al. 2000; Mikula et al. forthcoming). For instance, Mikula et al. (forthcoming) reviewed > 1500 such records for almost 240 species of diurnal birds (however, unlike actual paper, one case included multiple observations with several bat individuals and species there; the total number of such records for diurnal birds will be thus much higher) that were obtained by similar searching methodology. However, diurnal birds are not main bat predators due to different activity time, number of incidences for more important bat predators such as owls, small mammalian carnivores, and, in some regions, snakes should be thus higher (Speakman 1991; Sparks et al. 2000; Denisova 2004; Esbérard & Vrcibradic 2007). Although, according to my knowledge, no exhaustive global overview on bat predation by these animal groups has been published up to date. Comparable number of incidences (52) and species spectra (14) was recorded during global survey on bat-catching spiders that are, however, mainly passive bat hunters using their nets for bat catching (Nyffeler & Knörnschild 2013). Low number of recorded incidences for anamniotes thus indicates that bat predation by fishes and amphibians is probably very rare event occurring only in restricted number of species. Below, I discuss the most significant findings that shed light on patterns of anamniotic predation on bats.

Majority of bat predation records by anamniotes came from the New World; however, there was not such strong pattern of tropical distribution of predation attempts as in spiders (Nyffeler & Knörnschild 2013). In fishes, almost all records were located in North and South America, two regions with the highest global diversity of freshwater fishes (Pelayo-Villamil et al. 2015). Similarly, majority of bat-hunting incidences by amphibians were from Neotropical, Australian and Nearctic regions, which are again characterised by really high diversity of amphibians (AmphibiaWeb 2015b). In addition, the aforementioned regions belong to the areas with the highest global microchiropteran diversity (Hutson et al. 2001), a bat group where vast majority of identified bat victims belonged. The predominant distribution of bat-hunting attempts in these regions suggested that observed bat-hunting pattern could simply be a result of random predation, which just included predator species that on the basis of morphological and dietary characteristics are able to consume bats. There are, however, only few such incidences for African anamniotes, although there is relatively high diversity of bats and their predators. Very limited study efforts compared with areas in the New World and Australia where lots of researchers and naturalists are present could be a probable justification of this geographical bias.

Majority of bats recorded as victims of predation by fishes are known to live or forage in the vicinity of water bodies. *Erophylla sezekorni* (Phyllostomidae) roosts in hot caves, sometimes overhanging over the water surface (Yager & Williams 1988), Myotis grisescens and M. lucifugus forage over water surface when looking for insects (Harriman 2003; Havens 2006), and Noctilio leporinus (Noctilionidae) is known for its fish-eating habits (Börk 2006). In truth, there are not exceptional predation attempts by fishes on vertebrates, especially birds living or hunting near water sources (e.g. Glegg 1945; Oatley 1960). O'Brien et al. (2014) reported 20 cases of successful predation on swallow Hirundo rustica by tigerfish Hydrocynus vittatus. Among bats, similar case of predation was described by Börk (2006) who observed one attempted capture of large fish on *N. leporinus* when skimming over water surface. Additional case of fish predation on bats involved large trouts (Salmonidae) and probably low-flying drinking bats (Murphy & Nichols 1913; Allen 1940). Although, I was not able to find any direct observations on similar hunting behaviour in other fish groups, it is very probable that it occurs also in Osteoglossidae family in which members are known as regular aerial feeders (Lowry et al. 2005). Predation on bats by fishes is, however, rarer than on birds, most probably due to the fact that even bats living near water are in direct contact with water only for short time unlike birds that are capable of swimming on water surface, diving or rising their juveniles there.

Several bat species recognised as amphibian prey are known to feed near to the ground or water surface (e.g. Myotis austroriparius and M. mystacinus) (Jones & Manning 1989; Tamling 2004), roosting in caves in large aggregations (e.g. M. australis, Pteronotus personatus) (Means 2003; de la Torre & Medellín 2010) or in human buildings (Molossus molossus) (Kunz & Reynolds 2003). There are observations of bat catching by frogs when bat foraged very close to the ground surface (Torres 2013), near roosting places of bats such as caves (Means 2000, 2003; Cray 2007; Richards & Hall 2012) or consuming them in the vicinity of buildings (Petris 2011; Srpimentelbio 2015). Many bat species were, however, attacked when caught in mist nets; several frugivorous and nectarivorous bats, otherwise presumably immune to predation by amphibians, were thus attacked (Carollia perspicillata and Anoura caudifer, Glossophaga soricina, Lonchophylla mordax) (Ésberard et al. 2006; Castro et al. 2011; Filho et al. 2014). Majority of bat catches involved larger and considerably opportunistic frog

species. It is interesting to note that bat-hunting records for invasive *R. marina* and *R. catesbeiana* (http://www.invasive. org/species/amphibians.cfm, accessed 8 October 2015) represented one-third of all incidences for amphibians. It is assumed that invasive species of frogs can have broader trophic niche than native species (San Sebastián et al. 2015) with capacity to exploit more diverse dietary resources. Relatively high frequency of bats in their diet compared to other frogs can thus reflect their highly opportunistic nature of hunting.

It is noteworthy to say that not all cases of bat predation were completely accidental; some populations of anamniotes are probably able to regularly feed on bats. Among fishes, individuals of *L. griseus* were observed as systematically waiting under maternal colony of *E. sezekorni* for falling bats near the entrances of Lucayan cavern (26°36'N, 78°24'W), Bahamas (Yager & Williams 1988). In addition, frogs *R. marina* and *L. caerulea* were described as sitting around cave entrances in Australia and waiting for bats knocked to the ground by collision when emerging (Richards & Hall 2012). However, even in these cases where fishes and frogs catch bat relatively often, they predominantly prey upon few bat individuals only, including mainly fallen bats.

Finally, I can state that bat predation by anamniotes is rare, including only very limited number of fish, amphibian and bat species worldwide (> 1% of global diversity in majority of cases). There were only few cases where these predators were observed as systematically waiting for bats around their roosting sites. In these cases, long-term research may help us to understand potential effects of anamniotic predations on bats. However, with respect to the total number of recorded cases, bat-hunting activity of fishes and amphibian has most probably only very limited influence on bat populations and their behaviour in general.

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#### References

Allen, G.M. (1940) Bats. The Harvard University Press, Cambridge.

- AmphibiaWeb (2015a) Information on Amphibian Biology and Conservation. Retrieved from http://amphibiaweb.org/ (accessed 29 September 2015).
- AmphibiaWeb (2015b) Worldwide amphibian declines: How big is the problem, what are the causes and what can be done? Retrieved from http://www.amphibiaweb.org/declines/declines.html (accessed 9 October 2015).
- Arrington, D.A. & Arrington, J.L. (2000) Hyla boans (rusty tree frog). Diet. Herpetological Review, 31, 170.
- Barbour, R.W. & Davis, W.H. (1974) Mammals of Kentucky (Vol. 5). University Press of Kentucky, Lexington.
- Bierly, C. (1998) Photo Gallery. Retrieved from http://www.sitesalive. com/rl98s/private/gallery/web.htm (accessed 8 October 2015).
- Borell, A.E. & Ellis, R. (1934) Mammals of the Ruby Mountains region of north-eastern Nevada. Journal of Mammalogy, 15, 12-44.
- Börk, K.S. (2006) Lunar phobia in the greater fishing bat Noctilio leporinus (Chiroptera: Noctilionidae). International Journal of Tropical Biology and Conservation, 54, 1117-1123.

- Castro, I.J.D., Silva, C.R., Costa, A.J.S.D. & Martins, A.C.M. (2011) Opportunistic predation of *Artibeus planirostris* (Spix, 1823) and *Carollia perspicillata* (Linnaeus, 1758) (Chiroptera, Phyllostomidae) by marsupials and anuran in the APA do Rio Curiaú, Amapá State, Brazil. Acta Amazonica, 41, 171-174.
- Cray (2007) Green tree frog eats bat. Retrieved from https://aussiepythons.com/forum/showthread.php/59303-Green-Tree-Frogeats-Bat (accessed 22 September 2015).
- Creel, G.C. (1963) Bats as a food item of *Rana pipiens*. Texas Journal of Science, 15, 104-106.
- da Silva, L.A.M., dos Santos, E.M. & de Amorim, F.O. (2010) Predação oportunística de *Molossus molossus* (Pallas, 1766) (Chiroptera: Molossidae) por *Rhinella jimi* (Stevaux, 2002) (Anura: Bufonidae) na Caatinga, Pernambuco, Brasil. Biotemas, 23, 215-218.
- Davis, N. (n.d.) Frog eats bat. Retrieved from http://www.natgeotv. com.au/natgeosnap/4363-frog-eats-bat.aspx (accessed 29 September 2015).
- de la Torre, J.A. & Medellín, R.A. (2010) *Pteronotus personatus* (Chiroptera: Mormoopidae). Mammalian Species, 42, 244-250.
- Dean, L. (2008) What's for lunch? Retrieved from http://www.fws.gov/ fieldnotes/regmap.cfm?arskey=24229 (accessed 24 September 2015).
- Denisova, E.B. (2004) Позвоночные как естественные враги рукокрылых. [Vertebrates as enemies of bats]. Scientific notes of Taurida National V.I. Vernadsky University, Series "Biology and Chemistry", 17, 212-215.
- Esbérard, C.E. & Vrcibradic, D. (2007) Snakes preying on bats: New records from Brazil and a review of recorded cases in the Neotropical Region. Revista Brasileira de Zoologia, 24, 848-853.
- Esbérard, C.E.L., Jordão, T., Costa, L.M. & Bergallo, H.G. (2006) *Leptodactylus labyrinthicus* (labyrinthicus frog). Prey. Herpetological Review, 37, 204.
- Ferreira, F.S., Vicentin, W., Costa, F.E.D.S. & Súarez, Y.R. (2014) Trophic ecology of two piranha species, *Pygocentrus nattereri* and *Serrasalmus marginatus* (Characiformes, Characidae), in the floodplain of the Negro River, Pantanal. Acta Limnologica Brasiliensia, 26, 381-391.
- Filho, L.E., Feijó, A. & Rocha, P.A. (2014) Opportunistic predation on bats trapped in mist nets by *Leptodactylus vastus* (Anura: Leptodactylidae). Biotemas, 27, 205-208.
- FishBase (2015) Retrieved from http://www.fishbase.org/ (accessed 29 September 2015).
- Ford, F. (2013) Wild: 75 Freshwater Tropical Fish of the World. The Greenwich Workshop Press, Seymour.
- Froese, R. & Pauly, D. (2015) Brachymystax lenok. Retrieved from http://www.fishbase.org/summary/2079 (accessed 22 November 2015).
- Gonzalez-Fernandez, M. (2013) Retrieved from https://www.facebook. com/groups/Chiroptera.Bats/permalink/10153259529085392/ (accessed 29 September 2015).
- Gouveia, S.F., Rocha, P.A., Milkalauskas, J.S. & Silveira, V.V. (2009) *Rh-inella jimi* (Cururu toad) and *Leptodactylus vastus* (Northeastern pepper frog). Predation on bats. Herpetological Review, 40, 210.

- Gunnell, G.F. & Simmons, N.B. (2012) Evolutionary History of Bats fossils, molecules and morphology. Cambridge University Press, Cambridge.
- Harriman, V. (2003) *Myotis grisescens*. Animal Diversity Web. Retrieved from http://animaldiversity.org/accounts/Myotis\_grisescens/ (accessed 12 October 2015).
- Havens, A. (2006) *Myotis lucifugus*. Animal Diversity Web. Retrieved from http://animaldiversity.org/accounts/Myotis\_lucifugus/ (accessed 12 October 2015).
- Hermann, J.A. (1950) The mammals of the Stockton Plateau of northeastern Terrell County, Texas. The Texas Journal of Science, 2, 368-393.
- Hogan, Z. & Jensen, O. (2013) *Hucho taimen*. The IUCN Red List of Threatened Species 2013: e.T188631A22605180. Retrieved from http://dx.doi.org/10.2305/IUCN.UK.2013-1.RLTS. T188631A22605180.en (accessed 22 September 2015).
- Hutson, A.M., Mickleburgh, S.P. & Racey, P.A. (2001) Microchiropteran bats: Global status survey and conservation action plan. IUCN/ SSC Chiroptera Specialist Group. IUCN, Gland, Switzerland and Cambridge.
- Ingles, L.G. (1947) Mammals of California. Standford University Press, California.
- InTheory (2014) Comment. Retrieved from http://www.scientificamerican.com/article/fish-go-birding-video/ (accessed 28 September 2015).
- Jones, C. & Manning, R.W. (1989) Myotis austroriparius. Mammalian species, 332, 1-3.
- Jones, C.J. (1961) Additional records of bats in New Mexico. Journal of Mammalogy, 42, 538-539.
- Jones, R.S. & Hettler, W.F. (1959) Bat feeding by green sunfish. Texas Journal of Science, 11, 48.
- Kaimov, M.G. & Gairabekov, R.H. (2009) Трофические особенности и связанные с ними миграции ручьевой форели на территории Чеченской Республики. The South of Russia: Ecology, Development, 4, 97-99.
- Kinsey, C. (1961) Leopard frog attacks bat. Journal of Mammalogy, 42, 408-408.
- Kirkpatrick, R.D. (1982) Rana catesbeiana (bullfrog). Food. Herpetological Review, 13, 17.
- Korschgen, L.J. & Baskett, T.S. (1963) Foods of impoundment-and stream-dwelling bullfrogs in Missouri. Herpetologica, 19, 89-99.
- Kunz, T.H. & Fenton, M.B. (2003) Bat ecology. University of Chicago Press, Chicago.
- Kunz, T.H. & Reynolds, D.S. (2003) Bat colonies in buildings. Monitoring trends in bat populations of the United States and territories: problems and prospects (eds T.J. O'Shea & M.A. Bogan), pp. 91-102. US Geological Survey, Biological Resources Division, Information and Technology Report, USGS/ BRD/ITR-2003-003, Washington.
- Leblanc, F. (2005) Case of predation of a bat by a frog (genus *Rana*) in Creuse (Limousin, France). Rhinolophe, 17, 29.
- Lee, D.S. (1969) Notes on the feeding behavior of cave-dwelling bullfrogs. Herpetologica, 25, 211-212.

- Lesiński, G., Gryz, J. & Kowalski, M. (2009) Bat predation by tawny owls *Strix aluco* in differently human-transformed habitats. Italian Journal of Zoology, 76, 415-421.
- Lima, S.L. & Dill, L.M. (1990) Behavioral decisions made under the risk of predation: a review and prospectus. Canadian Journal of Zoology, 68, 619-640.
- Lowe, C.G., Wetherbee, B.M., Crow, G.L. & Tester, A.L. (1996) Ontogenetic dietary shifts and feeding behavior of the tiger shark, *Galeocerdo cuvier*, in Hawaiian waters. Environmental Biology of Fishes, 47, 203-211.
- Lowe-McConnell, R.H. (1964) The fishes of the Rupununi savanna district of British Guiana. Groupings of fish species and effects of the seasonal cycles on the fish. Zoological Journal of the Linnean Society, 45, 103-144.
- Lowry, D., Wintzer, A.P., Matott, M.P., Whitenack, L.B., Huber, D.R., Dean, M. & Motta, P.J. (2005) Aerial and aquatic feeding in the silver arawana, *Osteoglossum bicirrhosum*. Environmental Biology of Fishes, 73, 453-462.
- Macdonald, S. (2010) Gulf of Carpentaria. Retrieved from http://www. stewartmacdonald.com.au/blog/2010/05/gulf-of-carpentaria-2/ (accessed 29 September 2015).
- Means, B.D. (2000) Round the world 2001. Retrieved from http://www. brucemeans.com/photo\_world\_2001.htm (Accessed 22 September 2015).
- Means, B.D. (2003) Crack of doom. BBC Wildlife, 3, 55.
- Means, B.D. (2008) Stalking the Plumed Serpent and Other Adventures in Herpetology. Pineapple Press, Sarasota.
- Merritt, J.F. (2014) Guide to the Mammals of Pennsylvania. University of Pittsburgh Press, Pittsburgh.
- Mikula, P., Morelli, F., Lučan, R., Darryl, J. & Tryjanowski, P. (forthcoming) Bats as prey of diurnal birds: A global perspective. Mammal Review.
- Molinari, J., Gutiérrez, E.E., Ascenção, A.A., Nassar, J.M., Arends, A. & Márquez, R.J. (2005) Predation by giant centipedes, *Scolopendra* gigantea, on three species of bats in a Venezuelan cave. Caribbean Journal of Science, 41, 340-346.
- Murphy, R.C. & Nichols, J.T. (1913) Long Island fauna and flora I. The bats (Order Chiroptera). Science Bulletin of the Museum, Brooklyn Institute of Arts and Sciences, 2, 1-15.
- Murray, T. (2004) Bullfrog (*Rana catesbeiana*) eating a bat. Retrieved from http://www.pbase.com/tmurray74/image/33517067 (accessed 22 September 2015).
- National Geographic (2013) Catfish vs. bat. Retrieved from https:// www.youtube.com/watch?v=mDLh3\_gpOzo (accessed 24 September 2015).
- Nelson, J. (2006) Fishes of the World. 4th ed. John Wiley and Sons, New York.
- Nyffeler, M. & Knörnschild, M. (2013) Bat predation by spiders. PloS One, 8, e58120.
- Országhová, Z., Mikulíček, P. & Pachinger, K. (2003) Whiskered bat (*My-otis mystacinus*) as a prey of the edible frog (*Rana esculenta*). Biologia-Bratislava, 58, 291-291.
- Oatley, T.B. (1960) Miscellaneous notes of natural history interest. Swallows taken by tigerfish. Lammergeyer, 1, 37-38.

- O'Brien, G.C., Jacobs, F., Evans, S.W. & Smit, N.J. (2014). First observation of African tigerfish *Hydrocynus vittatus* predating on barn swallows *Hirundo rustica* in flight. Journal of fish biology, 84, 263-266.
- Parer, D. & Parer-Cook, R. (n.d. a) Bat frog. Retrieved from http://picsant.com/62537481-bat-frog.html (accessed 28 September 2015).
- Parer, D. & Parer-Cook, R. (n.d. b) White's tree frog (*Litoria caerulea*) feeding on little long-fingered bat (*Miniopterus australis*), central Queensland, Australia. Retrieved from http://www.gettyimages.ae/detail/photo/whites-tree-frog-feeding-on-littlelong-high-res-stock-photography/479668747 (accessed 28 September 2015).
- Pelayo-Villamil, P., Guisande, C., Vari, R.P., Manjarrés-Hernández, A., García-Roselló, E., González-Dacosta, J., Heine, J., Vilas, L.G., Patti, B., Quinci, E.M., Jiménez, L.F., Granado-Lorencio, C., Tedesco P.A. & Lobo, J.M. (2015) Global diversity patterns of freshwater fishes-potential victims of their own success. Diversity and Distributions, 21, 345-356.
- Petris, M. (2011) Sapo comendo morcego. Retrieved from https://www. youtube.com/watch?v=Qy-yDJA\_4ek (accessed 28 September 2015).
- Rechi, E. (2014) Aruanã Negra (*Osteoglossum ferreirai*). Retrieved from http://www.aquarismopaulista.com/osteoglossum-ferreirai/ (accessed 25 November 2015).
- Richards, G. & Hall, L. (2012) A Natural History of Australian Bats: Working the Night Shift. Csiro Publishing, Collingwood.
- Roulin, A. & Christe, P. (2013) Geographic and temporal variation in the consumption of bats by European barn owls. Bird Study, 60, 561-569.
- San Diego Zoo (2015) Goliath frog. Retrieved from http://animals. sandiegozoo.org/animals/goliath-frog (accessed 29 September 2015).
- San Sebastián, O., Navarro, J., Llorente, G.A., Richter-Boix, A. (2015) Trophic strategies of a non-native and a native amphibian species in shared ponds. PLoS ONE, 10, e013054.
- Schalk, C.M., Montaña, C.G., Klemish, J.L. & Wild, E.R. (2014) On the diet of the frogs of the Ceratophryidae: Synopsis and new contributions. South American Journal of Herpetology, 9, 90-105.
- Schätti, B. (1984) Fledermäuse als Nahrung von Schlangen. Bonner Zoologische Beiträge, 35, 335-342.
- Schwalbe, C. (2015) Bullfrog eating a bat in the San Bernadino National Wildlife Refuge in the Sonoran Desert. Retrieved from http:// armi.usgs.gov/gallery/detail.php?id=398 (accessed 22 September 2015).
- Schwartz, A. & Henderson, R.W. (1991) Amphibians and Reptiles of the West Indies: Descriptions, Distribution, and Natural History. University Press of Florida, Gainesville.
- Simpfendorfer, C. (1992) Biology of tiger sharks (*Galeocerdo cuvier*) caught by the Queensland shark meshing program off Towns-ville, Australia. Marine and Freshwater Research, 43, 33-43.
- Smokeyrobot (2014) Comment. Retrieved from https://www.reddit. com/r/science/comments/1uvn4l/first\_confirmed\_record\_ of\_a\_freshwater\_fish/cem699p (accessed 28 September 2015).

- Sparks, D.W., Roberts, K.J. & Jones, C. (2000) Vertebrate predators on bats in North America North of Mexico. Reflections of a naturalist. Papers Honoring Professor Eugene D. Fleharty (ed J.R. Choate), pp. 229-241. Fort Hays Studies, Kansas, USA.
- Speakman, J.R. (1991) The impact of predation by birds on bat populations in the British Isles. Mammal Review, 21, 123-142.
- Srpimentelbio (2015) Sapo x morcego. Retrieved from https://www. youtube.com/watch?v=7D7bBZDkxHU (accessed 28 September 2015).
- Tamling, J. (2004) Myotis mystacinus. Retrieved from http://animaldiversity.org/accounts/Myotis\_mystacinus/ (accessed 27 October 2015).
- Threlfall, C.G., Law, B. & Banks, P.B. (2013) Odour cues influence predation risk at artificial bat roosts in urban bushland. Biology Letters, 9, 20121144.
- Torres, P. (2013) What the heck is going on in this picture?. Retrieved from http://blog.perunature.com/2013/09/what-heck-is-goingon-in-this-picture.html (accessed 22 September 2015).
- Yager, J. & Williams, D. (1988) Predation by gray snapper on cave bats in the Bahamas. Bulletin Marine Science, 43, 102-103.